Biological Observations on a Subtidal *Mytilus californianus* Bed

BY

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(1 Text figure)

INTRODUCTION

AN INCREASING LITERATURE on sea mounts and submerged or emergent pinnacles suggests that these are interesting places departing often in surprising ways in expected biological structure, species composition and distribution pattern from that characteristic of the presumed continental source areas. There are few *a priori* reasons for anticipating these observed variances. For one, the Pacific shore of Western North America from at least Punta Baja, Baja California north to Glacier Bay, Alaska shows great overlap in the major community membership (RICKETTS, CALVIN & HEDGPETH, 1968; PAINE, 1969). In addition, the ecological processes responsible for the local patterns of distribution and abundance have been partially elucidated, and also appear constant (PAINE, 1966; PAINE & VADAS, 1969; EBERT, 1968; DAYTON, 1971; FEDER, 1959; CONNELL, 1970; HARGER, 1972). Why then should sea mounts and near-shore pinnacles be different? Although this contribution does not, and cannot, answer the question, it provides a longer and more extensive set of biological observations on two pinnacles in the mouth of Juan de Fuca Strait. In particular, I focus on the mussel, *Mytilus californianus* Conrad, 1837 since it is characteristic of the rocky intertidal zone, has been shown to be a competitively dominant species under exposed coastline conditions (PAINE, 1966; HARGER, 1972), and also can be a conspicuous member of the pinnacle fauna (SCAGEL, 1970; CHAN, 1973).

AREAS AND TECHNIQUES

The Northwest coast of Washington State, in particular the area adjacent to the Olympic Peninsula, is an exposed rocky shoreline characterized by heavy wave action during storms, violent subtidal surge, vigorous currents and a tidal range of about 10′ [3 m] (maximum on spring tides 11.3′ [3.39 m]; mean 8.0′ [2.4 m], ANONYMOUS, 1976) [1]. The range of offshore rocky structures examined varied from Tatoosh Island (124°44′ W; 48°23′ N), a 15 acre island with an extensive shoreline, to Duncan and Duntze Rocks (124°44′ W; 48°24.5′ N), pinnacles separated from both the mainland and Tatoosh by moderately deep (36 m) water, to Spike Rock (124°43′ W; 48°15′ N), another pinnacle close to shore. The locations of all these, and others referred to in the text, are given in the U. S. Geological Survey map, Cape Flattery quadrangle.

With the exception of Tatoosh, which has been the subject of an extensive shore-based investigation (PAINE, 1974), all the other sites must be visited by small boat and studied by SCUBA. This has not proven easy. The seasonally earliest examination made of Duncan Rock was 30 April 1973; the latest 25 September 1967. We sampled this area successfully on 9 occasions between September 1967 and June 1974; two visits were cancelled because of inclement weather and two other dives were made on secondary sites because of heavy swells or unabating current. Duntze Rock was sampled 5 times during the interval. Although my intention had been to pair the observations on these pinnacles, 3 dives on Duntze were aborted due to diver sickness or poor weather. This paired sampling was designed to compare these two adjacent pinnacles, one of which (Duncan Rock) is exposed at high water, the other of which rises to about −18′ [−5.4 m] at ELWS. Spike Rock was intentionally examined only once.

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[1] Tidal ranges and depths are given in feet to conform to usage in the standard tables (ANONYMOUS, 1976). Metric equivalents are added by the editor.

SUBTIDAL MUSSEL BEDS

Mytilus californianus is found on some (SCAGEL, 1970; CHAN, 1973) but not all (BIRKELAND, 1971) sea mounts. Despite being one of the most characteristic invertebrates in the rocky intertidal zone, it is uncommon or absent in the subtidal area immediately adjacent to large land areas. Dives off Tatoosh Island, Mukkaw Bay, Skagway Rocks, Spike Rock, Umatilla Reef and the north face of Cape Flattery failed to reveal subtidal mussel beds. On the other hand, mussels are abundant down to a depth of at least – 80′ [– 24 m] at Duncan and Duntze Rocks and were observed to occur to at least – 125′ [– 37.5 m].

Attempts were made to quantify 2 characteristics of these mussels, overall size distribution and percent cover of the primary substratum as a function of depth. The data for the former (Table 1) were gathered by divers collecting at known depths, scraping a known area of mussels into a "goodie bag." They suggest that the mussels comprising the matrix of the bed vary in size between 16.6 - 25.5 cm shell length. All size categories of mussels are represented. However, examination of the data by depth indicates that no small (< 2.0 cm) mussels were found below – 60′ [– 18 m], while the highest proportion (17%) were discovered in the shallowest (– 24′ [– 7.2 m]) sample. Although the data are too few for precise statements, it appears that larval recruitment is to the shallower portions of the bed. Recruitment may also be sporadic at these depths; an area on a rock wall cleared in September 1969 was inhabited solely by bryozoans one year later. It could not be relocated in subsequent dives.

Table 2 gives estimates of percent cover by depth. Cover appears solid on occupiable substrates at higher levels and diminishes rapidly at depths below – 70′ [– 21 m]. The high standard deviations around the mean values are in accord with the qualitative views of the divers; the mussels are patchily distributed in space, and their density diminishes with depth. The low value at – 55′ [– 16.5 m] was caused by large "bare" areas of rock that seemed potentially occupiable by mussels. No inter-year varia-

tions were recognized, even though many of the divers participated in a number of dives.

Although fewer data were obtained from Duntze Rock, the patterns of mussel distribution, body size and depth of occurrence were similar to those at Duncan Rock.

Table 1

Size (shell length, cm) distribution of *Mytilus californianus* at Duncan Rock, Washington. The right hand column gives data on the sizes of mussels being eaten by the local *Pisaster ochraceus*.

Mussel length (cm)	Resident population		Consumed by Pisaster	
	number	%	number	%
≤1.5	21	7.3		
1.6-2.5	15	5.2		
2.6-3.5	12	4.2	1	3.5
3.6-4.5	5	1.7		
4.6-5.5	13	4.5	1	3.5
5.6-6.5	9	3.1		
6.6-7.5	12	4.2		
7.6-8.5	9	3.1		
8.6-9.5	8	2.8	2	7.1
9.6-10.5	8	2.8	1	3.5
10.6-11.5	4	1.4		
11.6-12.5	6	2.1	2	7.1
12.6-13.5	5	1.7	2	7.1
13.6-14.5	9	3.1	3	10.7
14.6-15.5	9	3.1	2	7.1
15.6-16.5	12	4.2	1	3.5
16.6-17.5	17	5.9	1	3.5
17.6-18.5	17	5.9	1	3.5
18.6-19.5	22	7.7	1	3.5
19.6-20.5	19	6.6	3	10.7
20.6-21.5	20	7.0	3	10.7
21.6-22.5	13	4.5	1	3.5
22.6-23.5	10	3.5	2	7.1
23.6-24.5	6	2.1	1	3.5
24.6-25.5	4	1.4		
25.6-26.5	0	0		
≥26.6	1	0.3		

Table 2

Percent cover of subtidal surfaces as a function of depth by *Mytilus californianus* at Duncan Rock.

Water depth	−13′ [−3.9 m]	−25′ [−7.5 m]	−40′ [−12 m]	−55′ [−16.5 m]	−70′ [−21 m]
Number of samples	1	2	9	14	7
Mean % cover	100	98	76	28	62
Standard deviation	—	4	32	28	41

SUBTIDAL *Pisaster ochraceus*

These mussels represent an enormous potential resource for some predator. That species usually associated with intertidal mussel beds, preferring them as prey, and limiting their intertidal distribution is *Pisaster ochraceus* (Brandt, 1835) (FEDER, 1959, 1970; PAINE, 1966; LANDENBERGER, 1968; MENGE & MENGE, 1974). *Pisaster* occurs on Duncan and Duntze Rocks but is uncommon. This section provides quantitative data on *Pisaster* and offers some speculation on the causes of local density and body size variations.

Body Size: Just as the mussels, on the average, are large, so are the sea stars. Table 3 gives a histogram of all *Pisaster ochraceus* collected at Duncan (N = 59) and Duntze (N = 3) Rocks. The modal size is 3250 g wet weight although the mean (2643 g) is somewhat less. A significant point is that this average weight is almost an order of magnitude greater than that characterizing *Pisaster* populations found at selected intertidal sites within a 15 km radius (PAINE, in press). The large body size suggests an optimal or near optimal habitat, as might be anticipated by continual submergence (unlimited feeding time) and an abundance of suitable prey.

Table 3

Size distribution of subtidal *Pisaster ochraceus* at Duncan (N = 69) and Duntze (N = 3) Rocks in the mouth of the Strait of Juan de Fuca.

Size interval g. wet wt.	Number	Percent
0-499	1	1.4
500-999	4	5.6
1000-1499	8	11.1
1500-1999	10	13.9
2000-2499	12	16.7
2500-2999	13	18.1
3000-3499	15	20.8
3500-3999	4	5.6
4000-4499	3	4.2
>4500	2	2.8

Density: Estimates were obtained by haphazardly determining the position of a sampling station and then counting the number of *Pisaster ochraceus* within a quadrat. Quadrat dimensions varied from 7 to 50 m². The average density based on 21 quadrats at Duncan Rock was 10/577 or 0.017/m²; none was ever found within a quadrat at Duntze Rock. The densities are difficult to compare because these sea stars are rare, and a Fisher Exact Probability Test (SIEGAL, 1956) on those quadrats with and without *Pisaster* (6/15 at Duncan; 0/5 at Duntze) suggests no meaningful differences (p = 0.24). Another approach yields a different impression. I have divided the total number of *Pisaster* observed per dive at each area by diver effort. This assumes that neither more nor less time per diver was spent underwater at each location, and provides a means of correcting for total sampling effort. Since often fewer individuals participated in the second dive, such a procedure is necessary. The numbers of sea stars/diver/dive have then been ranked. For 14 data points, the highest 9 ranks all are for Duncan Rock, the lower 5 at Duntze. A Mann-Whitney U test (SIEGAL, 1956) rejects the null hypothesis of equal sea star/diver, p < 0.001, at the two stations. This significant difference is in agreement with the general diver impression and I accept it as reflecting a real biological difference between the two pinnacles.

CERTAIN INTERSPECIFIC RELATIONSHIPS

Pisaster – Mytilus: Table 1 shows the number and size of mussels being consumed by *Pisaster ochraceus*. There is no apparent maximal prey size limit enforced on the predator; rather, *Pisaster* appears quite capable of consuming those larger mussels forming the matrix of the bed. The predator does not consume *Mytilus* smaller than 8.5 cm in proportion to their abundance. Whether this is because they are generally protected within the matrix or because smaller prey are less appealing to a large predator is unknown. Other items consumed by *Pisaster* included one unmeasured mussel, 1 large *Balanus nubilis* Darwin, 1854 and 1 *Ceratostoma foliatum* (Gmelin, 1791), a carnivorous gastropod. In general, the diet appears limited to known preferred prey as should occur in the presence of abundant, large prey.

Mytilus – Epifauna: The subtidal *Mytilus* provide a substratum for a complex epifauna, the most conspicuous members of which are a sponge *Lissodendoryx firma* (Lambe, 1895), *Balanus nubilis*, an anemone *Epiactis prolifera* Verrill, 1869, the compound tunicate *Amaroucium* sp., and hydroids. These species collectively, but especially the tunicate and barnacle, were suspected to influence mussels negatively through overgrowth and eventual occlusion of the shell gape and siphonal areas. Many instances of partial overgrowth were observed, but recognizing and then obtaining completely overgrown and

therefore camouflaged specimens proved to be a challenge. Only 5 with the majority of the gape closed were obtained; 2 overgrown by combined *B. nubilis* and sponge, 2 by a tunicate and 1 by *Lissodendoryx*. By chance, all were found on September trips.

I have evaluated the influence of the "fouling community" as follows. Nine *Mytilus californianus* longer than 10 cm collected 9 September 1969 were measured (shell length), shucked, and then dried to a constant weight. These points and the regression line fitted by least squares are given in Figure 1. In addition, I have plotted the 5 points representing overgrown specimens. All the latter fall below the line, especially the 2 covered with *Amarou-*

cium and one with combined *Balanus nubilis* and sponge. The analysis suggests a detrimental influence. Whether it is reversible or not must depend on the species involved. The *B. nubilis* are not not heavily preyed upon by *Pisaster ochraceus* (although they may be by *Evasterias* or *Orthasterias*), and are clearly perennials. The sponges, tunicates and hydroids tend to have an annual growth periodicity that may provide the mussels with a reprieve. One *Mytilus* was found (at – 35′ [– 10.5 m]) to be enveloped in the holdfast of *Laminaria setchellii* (Silva, 1957); the latter was determined to be 5 years old on the basis of a growth ring analysis.

OTHER SPECIES

With the exception of *Pisaster ochraceus,* the fauna and flora of the pinnacles appeared quite similar. Other large sea stars were abundant. General agreement amongst divers was that the ranking by abundance would place *Dermasterias* at the top, followed by *Evasterias, Orthasterias, Pycnopodia, Stylasterias* and finally *Pisaster.* Henricia and *Leptasterias* were both abundant, but cannot be ranked because of their much smaller size. The carnivorous gastropods *Thais canaliculata* (Duclos, 1832) and *Ceratostoma foliatum* were abundant. Almost every mussel sample was festooned with small anemones (*Epiactis prolifera* and *Metridium senile* (Linnaeus, 1767)) and the shells overgrown with coralline algae, *Stylantheca porphyra* (Fisher, 1931) or *Balanophyllia elegans* (Verrill, 1864). The commonest crab was *Oedignathus.* Fish were always abundant.

A partial list of algal taxa is provided for completeness (courtesy of Dr. Lebednik). Browns include *Laminaria setchellii, Pleurophycus gardneri* (Setchell & Saunders, 1901), and one specimen of *L. longipes* (Bory, 1826), probably its southern-most occurrence. Encrusting red algae collected were *Melobesia marginata* (Setchell & Foslie, 1902), *Lithothamnium* or *Mesophyllum,* and *Serraticardia macmillani* (Silva, 1957). Other reds were *Botryoglossum farlowianum* (DeToni, 1900), *Callophyllis* sp., *Rhodymenia pretusa* (J. Agardh, 1851), *R. pacifica* (Kylin, 1931) and *Opuntiella californica* (Kylin, 1925). Although the list is surely incomplete, it probably is representative of the commoner algae. It, surprisingly, has no overlap with the 12 algal taxa recorded for Bowie seamount (53°18′ N; 135°39′ W) as recorded by Scagel (1970) and only one genus in common (of 4) with the flora of Cobb seamount (46°44′ N; 130°47′ W), as described by Birkeland (1971). On the other hand, the algal taxa for these latter places show some similarities.
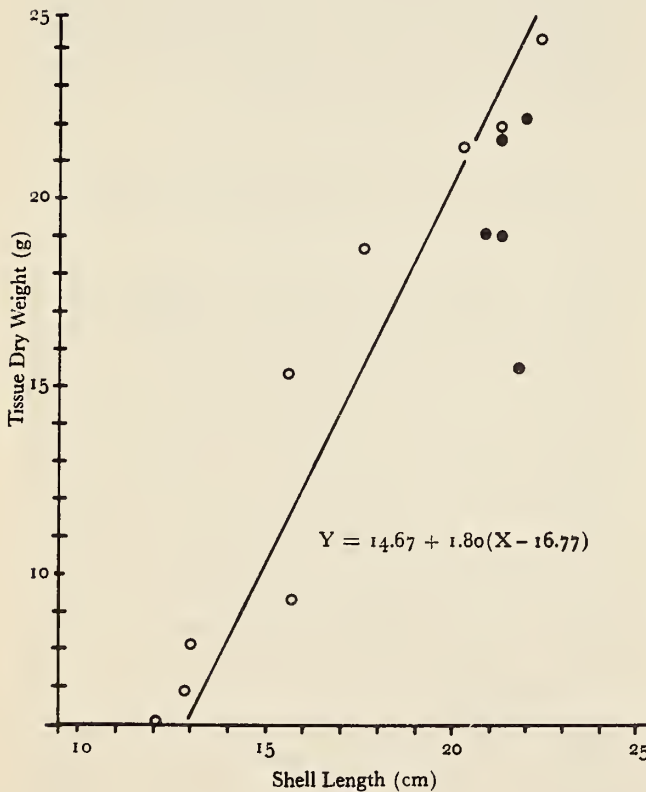

Figure 1

The shell length (cm) to dry body weight relationship for heavily (●) and lightly (○) encrusted *Mytilus californianus*. The linear regression, determined only from the former, suggests a negative influence on mussel body weight of a substantial epifauna. Note that the units of weight and length do not begin at zero

$$Y = 14.67 + 1.80(X - 16.77)$$

INTERPRETATION

One of the interesting geomorphological aspects of the area is the juxtaposition of an emergent and a continuously submerged pinnacle. Comparison of the biota of these suggests a single difference, although closer examination or better, basic biological knowledge of the constituent species could well suggest others. The number of *Pisaster ochraceus* varies from being low at Duncan Rock to almost non-existent at Duntze Rock. Although "nursery grounds" for this species have been described for more protected areas (MENGE & MENGE, 1974), no one to my knowledge has ever discovered a concentrated settlement of *P. ochraceus* on more exposed shorelines (FEDER, 1959, 1970; MANZEY, 1966; PAINE, 1974). When I have found small *Pisaster* on the Washington outer coast, it has always been in the lower intertidal zone, usually in crevices or on cave walls. Their observed diet has been almost entirely small barnacles (see also MENGE & MENGE, *op. cit.*), a resource that appears to reach peak abundances in the intertidal zones, and is a much less conspicuous and available component at depth, where they are readily overgrown by sponges, benthic algae and tunicates. The *Pisaster* density differences between the two pinnacles may provide a further clue to the behavior at settlement of *P. ochraceus*; that is, they should be expected at Duncan Rock and not at Duntze Rock if some attribute of the intertidal zone is important at settlement. *Pisaster* is abundant around Spike Rock, also emergent; it has not been recorded from either Cobb or Bowie seamounts, both of which are permanently submerged. Unfortunately, these limited data have generated no insights into why *P. ochraceus* settles so seldomly in exposed coastline habitat, and therefore cannot contribute answers to general questions on numerical regulation in this species. They do suggest, though, if the preceding conjecture was correct, that *Pisaster* is rare at Duncan Rock, despite the presence of a super-abundant prey resource, because of spatially-limited settlement opportunities. Conversely, the mussels may persist because their principal predator cannot establish its own dense population.

Another aspect of these observations deserves comment. Ecologists of necessity must focus on what a species' limiting resources are, and how they attain them or hold them against potential competitors. *Mytilus californianus* has been shown to be the winner in competitive encounters for space, a limiting requisite, on exposed shoreline situations (PAINE, 1966, 1974; HARGER, 1972). It forms monocultures in the intertidal zone and also, under particular circumstances, in subtidal environments and thus seems capable of excluding from the area other species requiring primary space. In the process, it provides a secondary substratum for both a species-rich fouling community and an association characteristic of the byssal threads and inter-mussel spaces.

The most restricted view of this competitive dominant would be that it was ecologically successful in, and best adjusted to, existence in the intertidal zone. Here, in the characteristic, often noted band, it encumbers from 20 to 100% of the available spatial resources. Departures from complete domination are generated by the wave-driven logs and other physical stresses so well documented by DAYTON (1971). An ecological description could state that mussels were occupying about 60% of the prime space, and therefore tended to be close to their saturation coverage. On the other hand, we know that the extent of potential coverage can be effectively doubled by predator removal experiments (PAINE, 1966, 1974) in which the 1.2 m wide band of mussels extends its limit lower by at least an additional 1.2 m. This suggests that *Mytilus californianus* is only at 30% of its saturation coverage, and that it is excluded from the remaining 70% by equally represented physical and predatory forces.

The existence of subtidal mussel beds demonstrates the capacity for competitive domination well below the limit that it is currently possible to achieve experimentally. It is conceivable that *Mytilus californianus* under totally benign (physically mild and predation-free) conditions could occupy the primary space between the tidal limits of +10′ [+3 m] to −90′ [−27 m]. That it does not do so, despite its demonstrated competitive abilities, indicates the difficulty of inferring a relationship between total spatial coverage and competitive ability, for in nature *M. californianus* appears capable of only occupying about 4% of its fundamental niche when the dimension in question is space.

ACKNOWLEDGMENTS

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